

# Functional Consequences of Phenotypic Plasticity in Echinoid Larvae

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**Abstract.** Phenotypic plasticity in feeding structures has been described for several larvae of marine invertebrates, including four species of echinoids. In these echinoids, larvae grown with scarce food grow a longer ciliated band than larvae grown with abundant food. Such phenotypic plasticity may be functionally significant if longer ciliated bands permit higher feeding rates when food is scarce. We replicate an earlier result showing that larvae of a sand dollar, *Dendraster excentricus*, grow longer ciliated bands in culture with scarce food. We show that these larvae can capture suspended food particles at the tips of longer arms, and that longer ciliated bands result in higher maximum clearance rates. The maximum clearance rate is enhanced by this phenotypic plasticity both early and late in larval life. However, longer ciliated bands did not completely compensate for reduced food supply: larvae grown with scarce food needed more time to complete larval development and metamorphosed into smaller juvenile sand dollars relative to larvae grown with abundant food.

## Introduction

Phenotypic plasticity of form and development can affect the evolution of structures, behaviors, and life histories (Newman, 1988; Stearns, 1989; West-Eberhard, 1989). Mechanisms that produce plasticity should evolve when an advantageous alternative phenotype is reliably signaled, the demand for the alternative form is unpredictable, and the cost of expressing the alternative phenotype is high (Harvell, 1990). Demonstrating the functional significance of induced forms or be-

haviors requires knowledge of the natural history of species and their interactions with mates, food, predators, and the environment (*e.g.*, Dodson, 1989).

Marine invertebrate larvae exhibit a phenotypic plasticity modulated by the abundance of planktonic food (*e.g.*, Strathmann *et al.*, 1993). The echinopluteus larvae of sea urchins and sand dollars develop as two compartments that are partly independent physiological and developmental units. The larval feeding structure is a band of ciliated epithelial cells borne on long larval arms (Strathmann, 1971). The beat of these cilia is responsible for swimming and feeding by larvae (Strathmann, 1971). In contrast, the postlarval structures develop as a disc-shaped rudiment on the left side of the larval stomach (Okazaki, 1975). The two structures are functionally and developmentally independent of each other: the juvenile rudiment is not functional until very late in larval life, and the ciliated band is dismantled during metamorphosis (Okazaki, 1975). In at least four species of echinoids, larvae respond to low food levels in laboratory culture (Boidron-Metairon, 1988; Hart and Scheibling, 1988; Strathmann *et al.*, 1992) and in the plankton (Fenaux *et al.*, 1994) by altering the allocation of scarce materials to the growth of the ciliated band and the juvenile rudiment: when food is scarce, larvae grow longer arms and ciliated bands, and development of the rudiment is delayed.

Phenotypic plasticity of ciliated band growth may be a common adaptation among larvae of echinoids: it is shared by members of the Clypeasteroidea and Echinoida, which diverged more than 200 million years ago (Wray, 1992). This type of plasticity of growth may have evolved more than once within the class, or it may be a shared ancestral feature of all extant echinoids. This plasticity has been assumed to be adaptive because it results in a larger feeding structure when food is scarce (Strathmann *et al.*, 1992). A measure of capacity for capturing food is

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the maximum clearance rate; clearance rate is the volume of water cleared of food per time. Ciliated band length is correlated with maximum clearance rate in comparisons among developmental stages of echinoid larvae (Strathmann, 1971; Hart, 1991). However, the effect of phenotypic plasticity of ciliated band growth on maximum clearance rates of plutei has not been measured.

We present an experimental test of the functional significance of phenotypic plasticity of ciliated band growth in echinoid larvae. (1) We show that larvae of the sand dollar *Dendraster excentricus* grow ciliated bands that are longer—in absolute length and in proportion to the size of the juvenile rudiment—when food is scarce (this effect of food on allometric growth of larvae was previously demonstrated for *Dendraster* by Boidron-Metairon, 1988). (2) The arms of plutei grow at the tips, and larvae with longer ciliated bands have grown longer arms by extending the arm tips. If particles cannot be caught near the arm tips, then variation in maximum clearance rates of larvae may be unrelated to or indirectly related to phenotypic plasticity of arm and band length. We show that larvae with longer arms and ciliated bands can capture particles at the tips of these longer arms. (3) Finally, we show that maximum clearance rates of larvae grown with scarce food are higher—in absolute units (early and late in development) and in relation to the growth of the juvenile rudiment (during most of the larval period)—than feeding rates for larvae grown with abundant food.

### Materials and Methods

Adult sand dollars were collected at a site north of Puget Sound near Olga, Orcas Island, Washington State. Gametes were obtained for two experiments by injecting adults with 0.5 M KCl on 12 and 20 April 1993. Within an experiment, all embryos and larvae for the experiment were full siblings, obtained from eggs of a single female and sperm of a single male. In the first experiment, eggs were 128  $\mu\text{m}$  in diameter (mean of 10 measurements, with all variation within  $\pm 4 \mu\text{m}$ , the unit of measurement). In the second experiment, eggs were 130  $\mu\text{m}$  in diameter (mean of 10 measurements, with variation not detectable within the 4- $\mu\text{m}$  units of measurement).

When larvae were nearly ready to begin feeding (near the end of the second day), they were divided among replicate jars, with an estimated 300 larvae per jar. The first experiment had three replicate jars per treatment; the second experiment had two replicate jars per treatment. Each jar contained 1.5 l of seawater that had been filtered through a 0.45- $\mu\text{m}$  membrane filter. The water was mechanically stirred by paddles pulled at 10 strokes  $\text{min}^{-1}$  (Strathmann, 1987). Jars were maintained at room temperature, which varied with the weather; but for the intervals of both experiments and for food treatments within

experiments, the mean temperatures (17.7–17.9°C) were similar, and the range of temperatures (16.5–19°C) was the same.

Water was changed every 2 days by removing more than 1.3 l from the jars and replacing it with water that had been filtered the day before and held at room temperature. Antibiotics were added at each water change for a concentration of 30  $\mu\text{g}$  penicillin  $\text{ml}^{-1}$  and 50  $\mu\text{g}$  streptomycin sulfate  $\text{ml}^{-1}$ .

At every water change, cells of the alga *Rhodomonas* sp. were added to achieve a total concentration of 5.0 cells  $\mu\text{l}^{-1}$  for high food in both experiments, 0.3 cells  $\mu\text{l}^{-1}$  for low food in the first experiment, and 0.25 cells  $\mu\text{l}^{-1}$  for low food in the second experiment. Three replicate jars were used for each food treatment. After the last observations on clearance rates and larval dimensions in the first experiment, the remaining larvae were reared to maturity for a test of competence for metamorphosis (food concentrations in the jars were not measured precisely during this period, but were approximately 5.0 or 0.3 cells  $\mu\text{l}^{-1}$ ). Experimental rearing for the first experiment was discontinued after testing for metamorphosis at 13 days of age (high food treatment) and 40 days (low food treatment). The second experiment was terminated when the animals were 9 days old.

The algal species and concentrations were selected on the basis of previous studies of echinoderm larvae. *Rhodomonas* has been determined to be a superior food for echinoplutei (Hinegardner, 1969; Leahy, 1986). With algae of similar size, echinoderm larvae reduced their clearance rates with more than 5.0 cells  $\mu\text{l}^{-1}$  (Strathmann, 1971), and grew at maximum rates at concentrations between 2 and 10 cells  $\mu\text{l}^{-1}$  (Lucas, 1982; Fenaux *et al.*, 1988); larvae of *D. excentricus* developed shorter arms and larger rudiments at 15 days of age when fed 6.0 cells  $\mu\text{l}^{-1}$  in contrast to 0.5 cells  $\mu\text{l}^{-1}$  (Boidron-Metairon, 1988).

We made videorecordings (30 frames  $\text{s}^{-1}$ ) of single, free-swimming larvae as they captured 15- $\mu\text{m}$ -diameter polystyrene spheres from suspension in 0.45- $\mu\text{m}$  membrane-filtered seawater. For most larvae, the concentration of spheres was 3  $\mu\text{l}^{-1}$ ; for some very large larvae, we reduced the concentration of spheres to 1 or 2  $\mu\text{l}^{-1}$ . Larvae were observed in a 63-ml chamber surrounded by a water-filled jacket that helped to buffer temperature changes during observation. Mean temperature  $\pm 1$  standard deviation (21.4  $\pm$  0.7°C) and the range of temperatures (20–23°C) for these observations were several degrees higher than those for larval rearing.

From these videotapes, we chose intervals of continuous swimming and feeding by each larva, and from these intervals we counted particle captures. We converted the counts of particle captures to clearance rates by dividing the time rate of capture by the concentration of spheres

in suspension. Because these intervals do not include periods when feeding was slow or ceased, our method estimates maximum clearance rate for these larvae.

We measured the following morphological features of each larva after removing it from the observation chamber: posterior body length (from the posterior end to the postoral transverse ciliated band), stomach length (anterior to posterior), juvenile rudiment diameter, and ciliated band length (see Strathmann *et al.*, 1992). Body and stomach lengths were used as measures of the growth and development of larval parts that are not involved in particle capture. All of these features were measured from camera lucida drawings. Ciliated band length was measured by McEdward's (1985) method for three-dimensional reconstruction. Our criterion for rudiment formation was contact between the invaginating epidermal surface (the amnion) and the left coelom.

Differences among jars and between the two experiments but within treatments (only high or only low food) were tested by Model I analysis of covariance (ANCOVA). Measures of larval dimensions or clearance rates were dependent variables, larval age was the independent variable, and effects of jars and the two experiments were combined into a single covariate. These tests are therefore equivalent to comparisons of growth or increase in feeding rate during development among five different groups of larvae treated similarly (though reared in different containers or at different times). Because we assessed five simultaneous comparisons within each food treatment (four morphological variables and clearance rate), we discounted the usual alpha value for these tests by the sequential Bonferroni correction for multiple contrasts (Rice, 1989). There were no significant differences among jars or experiments (estimated as the interaction between larval age and the jar covariate) at either high or low concentrations of food. Plots of data for larval dimensions and clearance rates indicated no differences among jars or between experiments. Because effects of jars or experimental runs were not evident in statistical tests and inspection of plots, plutei from replicate jars and from the two experiments were lumped within treatments in the analysis of effects of high and low food.

Effects of food on larval dimensions and clearance rates were first tested with the interaction between food level and larval age included in a Model I ANCOVA. In these tests, if effects of the interaction were not significant ( $P \geq 0.063$ ) and the  $F$  ratio for the interaction was less than twice the value of  $F_{0.50}$  (Paull, 1950), we tested for effects of food level and age without including the interaction term in the ANCOVA model.

The relationships among rudiment diameter, stomach length, ciliated band length, and clearance rate were compared for the two food treatments in a Model II ANCOVA using the method of Hess (1993). Slopes were compared

by a Student's  $t$  test (Clarke, 1980; McArdle, 1988). Elevations were not considered different if one elevation fell within the asymmetrical 95% confidence limits of the other.

Analyses of variance and covariance assume linear relationships between dependent and independent variables. In some cases, these bivariate relationships appeared nonlinear. We tested linearity in these plots by fitting quadratic regressions to each curve and estimating the value of the second-order coefficient in these regressions. For 18 simultaneous tests (Figs. 1, 2, 4, 5), we discounted the usual alpha value by the Bonferroni correction. We found four cases of significant nonlinear relationships: between ciliated band length or stomach length and larval age for larvae fed the smaller ration (Fig. 1A, B), and between maximum clearance rate and larval age for both groups of larvae (Fig. 4A). In the first two cases, we restricted our analysis of covariance to one portion of the data set (for larvae <10 days old) in which band length and stomach length increase linearly with age. In the other cases (Fig. 4A), we could not find an appropriate solution because both bivariate relationships were nonlinear but the curves differed in shape: that for larvae fed the larger ration was concave up (the second-order coefficient was significant and >0), and that for larvae fed the smaller ration was concave down (the second-order coefficient was significant and <0). We do not know of a single transformation that will render both relationships linear. We present the analysis of covariance of the untransformed data, acknowledging that this particular comparison violates an assumption of the test.

Metamorphosis of larvae from the first experiment was induced by exposure of larvae to materials associated with adult sand dollars. Sand from an aquarium with adult sand dollars was mixed with a small amount of water. Water and fine debris were then passed through a 70- $\mu$ m-mesh sieve into bowls. Each bowl received larvae from a different jar, with initially an estimated 120 larvae per bowl. Larvae were exposed to water from adult sand at 13 days of age (high food treatment) or at 40 days (low food treatment). Remaining larvae and metamorphosed juveniles were counted the next day. We also measured the lengths of the tests of juveniles. We compared test diameters of juveniles in a nested analysis of variance, with jars nested within food treatments.

## Results

### *Growth and development*

The effects of algal food concentration on relative growth of the ciliated band of *Dendraster* larvae have been described previously by Boidron-Metairon (1988). Our measurements of larval growth and development in response to algal food are similar to hers. Though our mor-

phological results are not new, we present them in detail to show the basis for the observed differences in feeding capabilities of larvae.

Each of the four morphological measurements increased during larval development, and growth rate for each measurement varied significantly with food ration. Ciliated band length, stomach length, midline body length, and juvenile rudiment diameter increased more rapidly with larval age for larvae fed the larger food ration (Fig. 1). In the last case, the age of onset of rudiment formation was also delayed by several days for larvae fed the smaller ration. In each case, the statistical interaction between larval age and food ration was highly significant ( $F_{1,d} > 51.90$ ,  $P < 0.001$ ), where the denominator degrees of freedom (d) was 97 for larval dimensions (77 when only larvae <10 days old were considered; see Materials and Methods above) and 50 for rudiment diameters (the analysis of rudiment diameters included only those larvae in which rudiment formation had begun).

Growth of the ciliated band with respect to food ration was slightly more complex than growth of the other morphological measures. For older larvae (>7 days old), those fed the larger ration grew faster and therefore had longer ciliated bands, and there was a significant main effect of food ration on band length ( $F_{1,43} = 18.268$ ,  $P < 0.001$ ) (the interaction between food ration and larval age was not significant;  $F_{1,42} = 3.616$ ,  $P = 0.064$ ). However, for younger larvae (<7 days old), there was no significant interaction between food ration and larval age ( $F_{1,52} = 3.071$ ,  $P = 0.086$ ). The main effect of food ration on band length in the ANCOVA was not significant ( $F_{1,53} = 1.864$ ,  $P = 0.178$ ). This result suggests that larvae fed very small rations are initially capable of developing feeding structures as large as those of larvae fed larger rations.

A surprising difference is hidden in the apparent similarity of ciliated band lengths for larvae <7 days old from the two food treatments. If only the youngest larvae (3 days old) are considered, ciliated bands were significantly

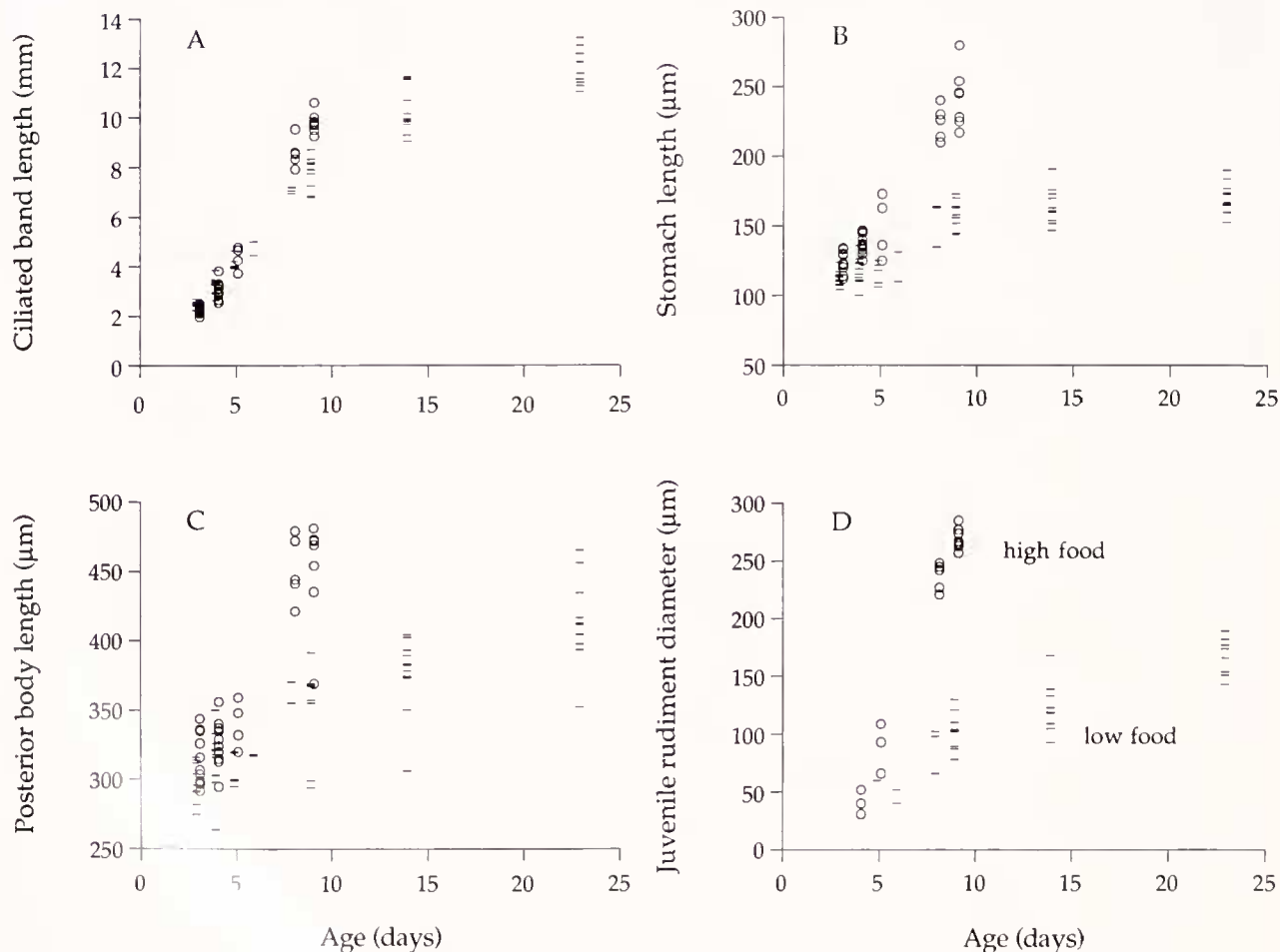


Figure 1. Growth of *Dendroaster excentricus* larvae fed a small (250 or 300 cells  $\text{ml}^{-1}$ ) or a large (5000 cells  $\text{ml}^{-1}$ ) ration of *Rhodomonas* sp. Bars show larvae fed the small ration; circles show larvae fed the large ration. For clarity, values for different food rations on a single day are offset by  $\pm 0.2$  days. A. Ciliated band length. B. Stomach length. C. Posterior body length. D. Juvenile rudiment diameter.

Table 1

Ciliated band lengths and maximum clearance rates of 3-day-old *Dendroaster excentricus* larvae fed different concentrations of algal food (*Rhodomonas* sp)

Food ration (cells ml <sup>-1</sup> )	Ciliated band length (mm)	Maximum clearance rate ( $\mu\text{l min}^{-1}$ )
5000	2.28 $\pm$ 0.16	1.60 $\pm$ 0.29
300	2.46 $\pm$ 0.16	1.91 $\pm$ 0.29

Each entry is mean  $\pm$  1 standard deviation for 11 cases. Both comparisons (between food rations) are statistically significant ( $P < 0.02$ ).

longer for those grown with scarce food than for those with abundant food (Table 1) ( $t = 2.946$ ,  $P = 0.008$ ). This comparison gives the clearest example of altered allocation of materials to the feeding structure in response to food ration: the absolute length of ciliated band can be greater for larvae growing with scarce food. Because larvae fed the larger ration grew faster, this early difference in size was not apparent when all larvae 3–7 days old were considered.

In our experiments, many larvae fed the larger ration were capable of metamorphosis when 13 days old, and few of these larvae grew ciliated bands  $> 10$  mm (Fig. 1D). In contrast, larvae fed the smaller ration required much more time to reach metamorphic competence, and they continued to grow longer ciliated bands (up to 13.2 mm). Ciliated bands of all 23-day-old larvae from these cultures were longer than the longest bands measured for any larvae fed the larger ration.

*Dendroaster* larvae also showed potential for allometric growth of the ciliated band relative to other parts of the

posterior body in response to differences in food ration. Band length was greater relative to stomach length (for all larvae, Fig. 2A) or to rudiment diameter (for older larvae in which rudiment development had begun, Fig. 2B). There was a significant interaction between stomach or rudiment size and food ration (for both comparisons,  $t > 4.81$ ,  $P < 0.001$ ). In this sense, larvae fed the two different food rations follow different physiological rules for allocation of materials into growth of the feeding structure and the postlarval structures: if these allocation rules were fixed, then the two sets of data in Figure 2A or 2B should coincide. As a consequence of altering these allocation rules, larvae fed a smaller food ration develop a larger feeding structure relative to the growth of postlarval parts, and the feeding structure eventually grows larger in absolute size than the feeding structures of larvae fed a larger ration.

#### Particle capture at arm tips

*Dendroaster* larvae fed either ration could capture polystyrene spheres at the arm tips. Figure 3, for example, shows a sphere captured at the tip of the right postoral arm of a 14-day-old larva feeding at  $11.5 \mu\text{l min}^{-1}$ ; this sphere made contact with the ciliated band twice more, at locations progressively nearer to the mouth, before it was ingested. The sequence of events (from initial capture to ingestion) took about 1.7 s (51 video frames), and the particle was transported about  $700 \mu\text{m}$  from the tip to the base of the arm. This capture (and others like it) resembles particle captures described previously (Strathmann, 1971; Hart, 1991) and occurs by the localized reversal of the beat of cilia (Strathmann *et al.*, 1972; Hart, 1990).

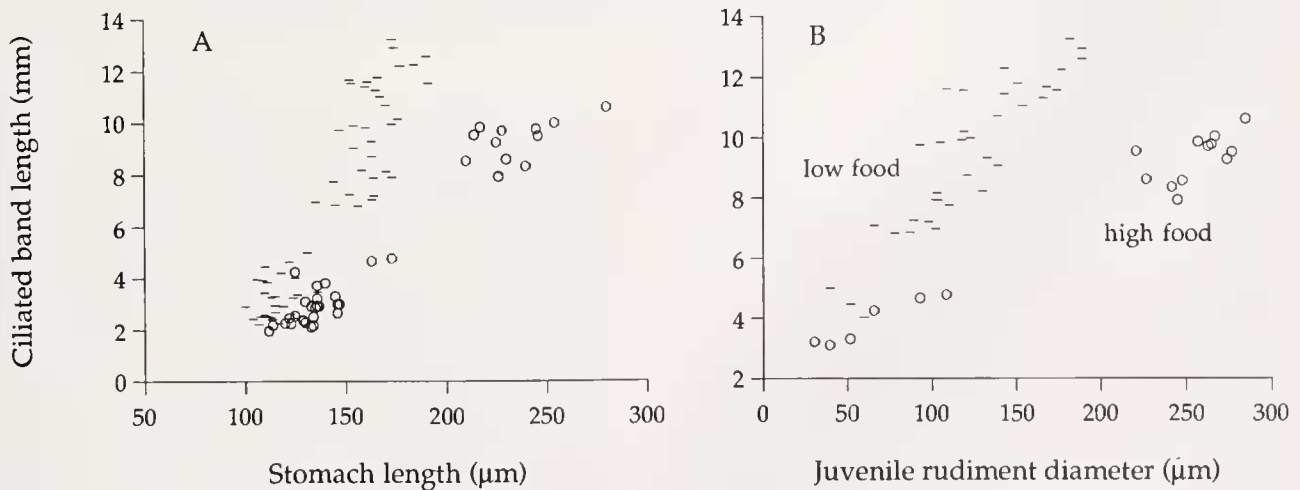
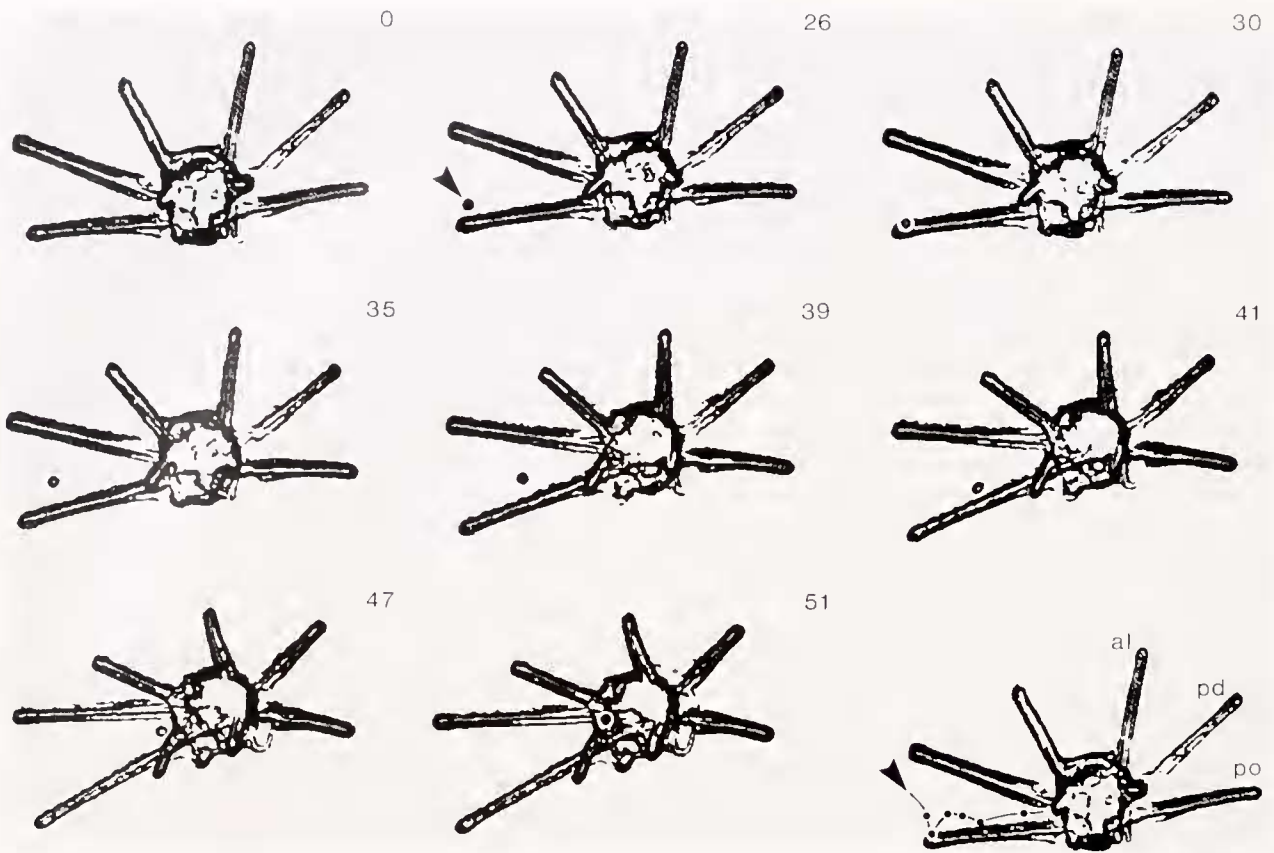


Figure 2. Ciliated band lengths relative to other measures of size of *Dendroaster excentricus* larvae fed a small (250 or 300 cells ml<sup>-1</sup>) or a large (5000 cells ml<sup>-1</sup>) ration of *Rhodomonas* sp. Bars show larvae fed the small ration; circles show larvae fed the large ration. A. Ciliated band lengths relative to stomach length. B. Ciliated band lengths relative to juvenile rudiment diameter.



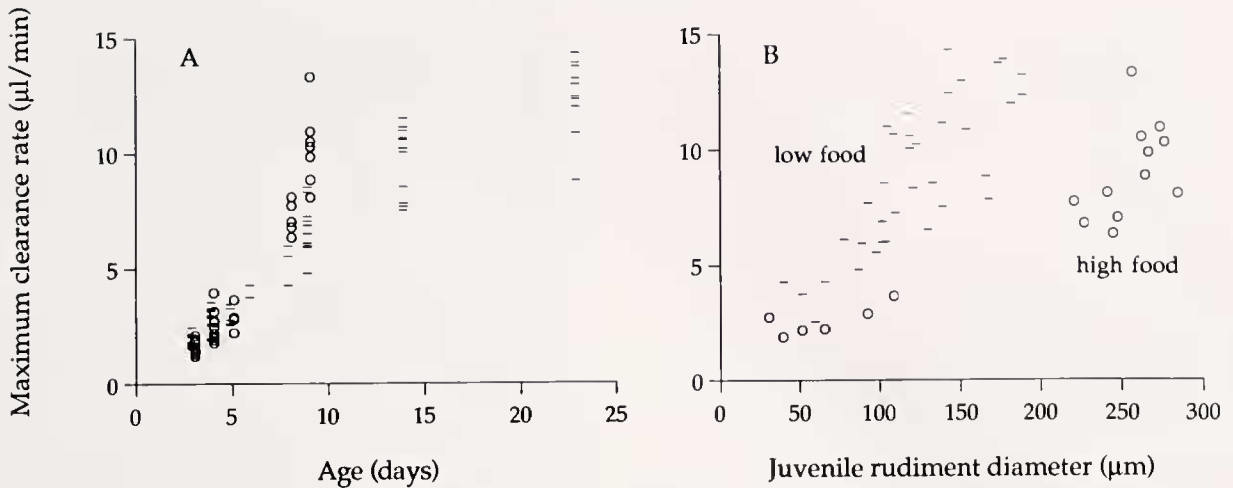
**Figure 3.** Capture of a polystyrene sphere by an 8-day-old *Dendraster excentricus* larva fed 250 cells  $\text{ml}^{-1}$  *Rhodomonas* sp. The larva is shown in anterior ventral view (swimming up toward the video camera). Video frame number (30 frames  $\text{s}^{-1}$ ) is shown in the upper right of each panel. Each video frame was edited to enhance contrast and reduce background pixel values to near zero. An unintended result of this editing is an increase in the apparent size of the polystyrene sphere (by about 2 $\times$ ). The sphere (arrow) came into focus at frame 26, was captured with a localized change in direction of the ciliary current at the tip of the right postoral arm (30–35), moved toward the larval midline (39), was captured again midway along the length of the arm (41–47), and was ingested (51). Inset (lower right): interpolated path of the captured sphere begins at the arrow; dots show the location of the sphere in frames 26–47. For scale, the right postoral arm is about 700- $\mu\text{m}$  long (actual scale is not known). Abbreviations: al, anterolateral arm; pd, posterodorsal arm; po, postoral arm.

### Clearance rates

Maximum clearance rates of echinoderm larvae are highly correlated with ciliated band lengths (Strathmann, 1971; Hart, 1991). Developmental changes in feeding rates of *Dendraster* larvae were associated with changes in band length (Fig. 4A). For larvae  $>7$  days old, there was a significant interaction between the effects of food ration and larval age on maximum clearance rate ( $F_{1,42} = 9.497$ ,  $P = 0.004$ ). Clearance rates increased more rapidly with age for larvae fed the larger ration, because these larvae rapidly grew ciliated bands at an early age. However, larvae fed the smaller ration eventually grew longer bands, and their clearance rates surpassed those of the largest larvae fed the larger ration. Mean maximum clearance rates of 23-day-old larvae ( $12.46 \pm 1.63 \mu\text{l min}^{-1}$ ,  $n = 10$ ) fed the

smaller ration were significantly greater than clearance rates of 9-day-old larvae fed the larger ration ( $10.28 \pm 2.80 \mu\text{l min}^{-1}$ ,  $n = 7$ ) ( $t = 2.687$ ,  $P = 0.017$ ). For larvae  $<7$  days old, there was no significant interaction between the effects of food ration and larval age on maximum clearance rate ( $F_{1,52} = 0.315$ ,  $P = 0.577$ ) and no significant main effect of food ration ( $F_{1,53} = 3.603$ ,  $P = 0.063$ ).

The functional significance of increased ciliated band length for larvae developing with scarce food is most evident from two comparisons: (1) maximum clearance rates of 3-day-old larvae with different band lengths, and (2) maximum clearance rates of larvae as a function of development of the postlarval structures. First, for 3-day-old larvae, clearance rates of larvae fed the smaller ration were significantly higher than those of larvae fed the larger



**Figure 4.** Maximum clearance rates of *Dendroaster excentricus* larvae fed a small (250 or 300 cells ml<sup>-1</sup>) or a large (5000 cells ml<sup>-1</sup>) ration of *Rhodomonas* sp. Bars show larvae fed the small ration; circles show larvae fed the large ration. A. Clearance rates for larvae of different age. B. Clearance rates relative to juvenile rudiment diameter.

ration (Table I) ( $t = 2.543$ ,  $P = 0.019$ ). This difference demonstrates that the earliest manifestation of phenotypic plasticity in these larvae is accompanied by a measurable increase in feeding rate for larvae with scarce food. Second, at any stage of development of the juvenile rudiment, clearance rates of larvae fed the smaller ration were substantially higher than those of larvae fed the larger ration (Fig. 4B), and there was a significant interaction between the effects of food ration and rudiment diameter on feeding rate ( $t = 4.927$ ,  $P < 0.001$ ). A qualitatively similar result is obtained if stomach length or posterior body length is used as the index of growth and allocation to the development of postlarval structures. This difference demonstrates the functional consequences of altered rules for allocation of scarce materials within the larva later in development.

Growth with scarce food might have other effects on maximum clearance rate than an increase in ciliated band length, but we have no evidence of such additional effects. Maximum clearance rates increased with ciliated band length for larvae fed both rations (Fig. 5), and the relationship between feeding rate and band length was not significantly different between the two groups. There was no significant interaction between the effects of band length and food ration ( $t = 0.208$ ,  $P > 0.50$ ) and no significant main effect of food ration (the 95% confidence intervals around the estimated regression intercepts overlapped broadly, and the confidence intervals of each estimate included the estimated intercept of the other). This result suggests that maximum clearance rates per length of ciliated band are similar for larvae following different allocation rules for the growth of larval and postlarval parts. The only functional differences between larvae fed

the two rations are that larvae fed the smaller ration allocate more material to the growth of the ciliated band, develop higher clearance rates at any stage of the development of postlarval structures, and eventually grow very long ciliated bands and develop very high feeding rates.

#### *Survival and metamorphosis*

The high survival rate in the cultures indicated that the observed differences in growth, allocation, and feeding rate were the result of developmental plasticity, not selective mortality of different genotypes at different concentrations of food. In the first experiment, survival—when adjusted for larvae removed for observation—was close to 100% at day 13 with both high and low concentrations of food. (Errors in the initial count resulted in a 5% apparent increase in larvae.) Survival remained high during continued observations of larvae in the three jars at the low concentration of food, with 78 to 81% survival over the next 23 days. In the second experiment, survival in the four jars was 88 to 98% on day 9, at the termination of the experiment.

Larvae from the first experiment were tested for competence for metamorphosis. More larvae proved competent at 13 to 14 days with abundant food than were competent at 40 to 41 days with scarce food, though the stimulus from the adult sand could also have differed (Table II). This result confirmed that the larvae on the smaller ration did develop more slowly toward competence for metamorphosis and did attain competence eventually. Larvae with abundant food formed larger juvenile tests than did larvae with scarce food (Table II). There were significant differences in test diameter among replicate

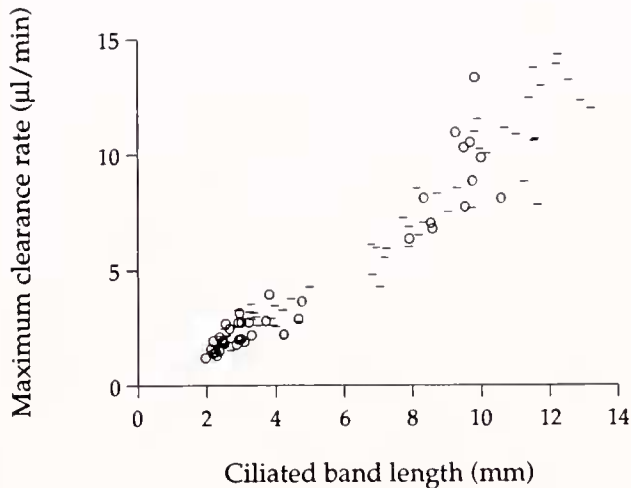


Figure 5. Maximum clearance rates relative to ciliated band length of *Dendroaster excentricus* larvae fed a small (250 or 300 cells ml<sup>-1</sup>) or a large (5000 cells ml<sup>-1</sup>) ration of *Rhodomonas* sp. Bars show larvae fed the small ration; circles show larvae fed the large ration.

jars ( $F_{3,95} = 6.051$ ,  $P < 0.001$ ). In spite of this variation among jars, tests of individuals from the high food ration were significantly larger than those from the low food ration ( $F_{1,3} = 15.943$ ,  $P = 0.028$ ). The difference in test diameter appears to have resulted from differences in food for larvae rather than from different stages in the competent period, because percent metamorphosing was not related to mean test length.

### Discussion

Our observations on form, particle captures, and clearance rates of *Dendroaster* larvae demonstrate that phenotypic plasticity of arm growth and ciliated band length in plutei is functionally significant: it increases feeding rate when food is scarce. Plutei grow longer arms and ciliated bands, while the growth of the postlarval parts is delayed. The lengthened portions of the arms can capture particles, and thus clearance rates are increased absolutely and in relation to the development of postlarval parts.

We found phenotypic plasticity of larval growth at two stages of development. Early in development, larvae growing with scarce food were able to grow longer ciliated bands than were larvae of the same age with abundant food, after only one day of feeding. Late in development, larvae with scarce food also grew longer ciliated bands than did larvae with abundant food, but this difference did not appear until after larvae with abundant food had completed development and metamorphosis. This late difference in size must result from altered allocation of materials acquired during larval feeding. The contrast between results for early and late larval stages suggests that the scope for phenotypic plasticity early in development

may depend on egg size, whereas the scope for plasticity later in development may depend on factors such as the efficiency of food digestion and assimilation.

Under the conditions of our experiment, increased growth of the ciliated band did not completely compensate for differences in amount of food: larvae feeding on the smaller ration took longer to complete larval development through metamorphosis and became smaller juveniles. Phenotypic plasticity of ciliated band length increased clearance rates of larvae feeding on the smaller ration, but we do not know whether this plasticity results in faster development than could occur with a fixed pattern of ciliated band growth when food is scarce. If so, then phenotypic plasticity of ciliated band growth might be adaptively (as well as functionally) significant. For example, such compensation might account for some of the observed insensitivity of larval growth to food abundance in the wild (see Olson and Olson, 1989).

The adaptive significance of this phenotypic plasticity in echinoplutei could be tested by comparing development times and postmetamorphic sizes for larvae following two different growth rules under the same conditions of scarce food: one rule favoring growth of the ciliated band (the bars in Fig. 2B), and another rule favoring growth of the juvenile rudiment (the circles in Fig. 2B). Unfortunately, larvae cannot yet be induced to follow the second allocation rule when they are grown with scarce food. We suggest, however, that this may be accomplished by manipulation of thyroid hormones (THs). Chino *et al.* (1994) recently described effects of TH supplements on development of the juvenile rudiment of three echinoid species. They show that late-stage plutei can be induced to form the juvenile rudiment in a dose-dependent response to exogenous TH in the absence of algal food, and they suggest that much of the TH found in larvae originates in algal food (larvae appear to synthesize little TH).

Table II

*Metamorphosis of Dendroaster excentricus larvae fed high and low rations of food*

Food ration (cells ml <sup>-1</sup> )	Metamorphosed (%) <i>n</i> = 120	Test diameter (µm) <i>n</i> = 20
5000	68	341 ± 13
	58	336 ± 15
	22	352 ± 9
300	48	320 ± 11
	20	315 ± 15
	0	—

Larvae fed the high ration were 13 days old; larvae fed the low ration were 40 days old. Each entry is a result for one replicate jar. Test diameter (mean ± 1 standard deviation) does not include spines.



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